A DESCRIPTION OF MICROBDELLA BIANNULATA WITH ESPECIAL REGARD TO THE CONSTITUTION OF THE LEECH SOMITE.

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Perhaps the most noteworthy of a number of annelids collected in the mountain region of North Carolina during the summer of 1898 is the little leech about to be described. The form appears to be rare, as it was met with but once. On this occasion an even dozen were found attached in a close cluster to the axillary and pectoral regions of a large *Desmognathus nigra*. As the morphological interest attaching to these leeches was at once recognized (though unfortunately not until all had been killed), special efforts were made to add to the supply. Notwithstanding that several hundreds of the salamander host were examined, the examples first collected remain unique. The locality is a mountain stream on the Yonahlossee road, at an elevation exceeding 3,500 feet. In about one-half or more of the specimens the gastric cæca were distended with blood, apparently derived from the salamander on which they were found. During life they were sluggish, and remained huddled together in a contracted state, making but little attempt to creep about or even to extend themselves.

Falling naturally within the limits of the *Glossiphonidæ*, this is, I think, the smallest species of that family which has been discovered, the length of sexually mature individuals in a half-extended condition being only from four to five millimeters. But of much greater interest is the, up to the present time, entirely novel structure of the complete somites, none of which present more than two well-defined external rings and whose internal relations are such as to elucidate several points affecting the value and limitations of the typical leech somite. The Chinese leech *Torix mirus* Blanchard ('98) is scarcely larger than the salamander leech and approaches it very closely in the external structure of the somites, which are biannulate dorsally and triannulate ventrally. Nothing is yet known of its internal anatomy. A fur-

ther study of *Torix* may render unnecessary the establishment of the following genus:

MICROBDELLA gen. nov.

The complete somites each consist externally of two annuli, a smaller posterior, and a larger anterior, which bears the metameric sensillæ on its posterior part and the nephridiopores on its anterior part. There are five pairs of testes, of which the last is enlarged. Intersegmental septa are well developed between many of the somites.

Microbdella biannulata sp. nov. Pl. VI.

Description.—The body is strongly depressed and sharp at the margins, though less so than in many parasitic species of *Glossiphonia*, etc. The suckers, and more especially the posterior one, are large even for a species of parasitic habit. Measurements are of no great value, as the proportions vary so much with the degree of extension or contraction or according to the amount of food contained in the stomach, but the specimen figured, which had the cæca only moderately filled, and was about two-thirds extended, had the following measurements:

Length 6.3 mm.

Greatest width (XV) 2 mm.

Greatest depth (XVII) .6 mm.

Diameter of acetabulum 1.4 mm.

Of course the species may reach a larger size than that attained by the type specimens, as among leeches sexual maturity is no indication of full growth, but if these specimens were found in their normal habitat this seems improbable.

The large size of the posterior sucker (Pl. VI, figs. 1, 2 and 3) is an excellent adaptation for retaining a hold on the slippery skin of a salamander, and the region of the body to which the leeches were found fixed is that which would afford them almost the best protection, and from which they would be least likely to be swept away when the host is actively swimming or when it burrows amongst shingle and pebbles, as is the habit of its kind. The anterior sucker is not expanded laterally, but its posterior margin is largely free and mobile (figs. 2 and 3).

The small mouth is situated in the anterior part of the ventral surface of the sucker, apparently in somite II (fig. 2, *m*). Al-

most immediately dorsal to it, and in the posterior half of somite III, is a conspicuous median spot of black (really dark brown when strongly illuminated in sections) pigment in which the two eyes are embedded close together (figs. 1 and 3, *e*). So intimately united are they that they can be resolved only in good sections. They have the typical structure. The male pore is between somites XI and XII. This opening (figs. 2 and 3, ♂) is large and conspicuous and is frequently rendered still more obvious by the partial eversion of the atrium. The much smaller female pore (figs. 2 and 3, ♀) lies in somite XII in a line with the furrow which separates the major and minor annuli, although the furrow itself is not usually continued so far onto the ventral surface. In the usual position on the dorsal surface just above the acetabulum, the rather large anus is situated; it lies behind or partly within somite XXVII (figs. 1 and 3, *a*).

Sixteen pairs of nephridial pores (figs. 2 and 5, *np*) have been definitely located on the ventral surfaces of the corresponding number of somites from VII to XXII inclusive. A seventeenth pair was sought, but not found, on somite XXIII, but owing to the proximity of this region to the acetabulum the integument is here much wrinkled, and they might readily have been overlooked in the several specimens examined. In the middle region of the body the pores are distinctly visible in surface views, and in sections the entire series can be readily traced, although the vesicles are so small that they rarely extend through more than two or three transverse, or twice that many longitudinal sections. Their position in the somite is of greater interest. The two pores of each pair are separated in the example figured by a distance which is approximately equal to one-half of the entire width of the body, but this distance necessarily varies with the shape of the body resulting from the greater or less distension of the gastric cæca. Antero-posteriorly they lie a little cephalad of the middle of the major annulus, their position being often marked by a very faint groove, which may extend nearly the width of the body.

The typical complete somites (figs. 1, 2 and 3) of this genus, as previously stated, consist of two distinct annuli, but these are generally sharply defined only on the dorsal surface and even here the furrows which separate them are much less deep than those separating successive somites. Ventrally the interannular furrows are

complete on a few of the anterior somites (VI to VIII, or thereabouts) only (fig. 2). Elsewhere they are much interrupted or extend only a little way mesiad from the margin. Not infrequently in longitudinal sections of contracted specimens a slight depression indicates the presence of traces of a faint furrow suggestive of incipient subdivision of the major annulus. This may occur not on the ventral side only, as noted above, but also dorsally, and always anterior to the line of sensillæ. The complete somites are, however, always strictly biannulate above and in most cases practically uniannulate below.

The metameric sensillæ (figs. 1 and 2) are rather small, and their arrangement could be worked out only partially in surface views of alcoholic specimens; the gaps were completed after the study of sections. In figs. 1 and 3, the rows of small circles, which do not accurately indicate the relative sizes of the several sense organs, show the typical distribution as finally determined. On fig. 2 those sensillæ only are shown which were seen in a single surface view, and they are represented as too large. They were found in sections in corresponding positions of other somites, but were not plotted. The dorsal median and inner lateral series are the best developed and, in fact, the sensillæ of these rows are the only ones which certainly have the typical structure, the others very frequently lacking the clear vitreous cells. It is worthy of comment in connection with Whitman's suggestion of the homology of these vitreous cells with epidermal glands that cells of the latter character are frequently associated with these smaller sensillæ. The six dorsal sensillæ occur constantly in all of the material examined, but the marginal organs are sometimes missing from one or more of the middle somites, and constantly so from somites I, II and III, and from two or three of the preanal somites, at least they could not be detected in sections. Of the small and inconspicuous ventral sensillæ, but two series were found on each side, whose position suggests the median and outer lateral. They are not entirely constant, even on the middle body region, one or more not infrequently being absent from a somite. The twelve sensillæ of each somite form a ring, the two halves of which are widely separated by a median interspace which is somewhat wider ventrally than dorsally. This ring encircles the major annulus half-way between the nephridiopores and the posterior margin of the annu-

lus. There are nineteen (Nos. V to XXIII inclusive) complete somites of the character just described, except, of course, that the first two and apparently the last lack nephridiopores.

Somites of a simpler character are found at both the anterior and posterior ends of the animal. At the anterior end they are related to the sucker (figs. 1 and 3). Somite V, the first of the biannulate ones, is much crowded ventrally by the posterior margin of the sucker, which is constituted of somite IV. The subdivision of the latter somite into rings is evident on the dorsal aspect only, where the shallow furrow fades and disappears a short distance from the median line, and is very faint at the margins. The line of sensillæ is placed much closer to the middle of the whole somite than is the case in the biannulate somites and the marginal pair is absent. In somite III all trace of subdivision into rings is wanting, the inner and outer lateral sensillæ lie exactly along the middle of the one simple ring, while the median pair have risen to the importance of eyes, which have moved to the posterior margin of the somite. Somite II is also a simple undivided ring, as much narrower than III as the latter is narrower than IV. Its anterior bounding furrow is so shallow as to separate it only imperfectly from the prostomium. But two pairs of distinct sensillæ remain on this somite, being those of the inner lateral and median series.

On the prostomium (figs. 1 and 2) anterior to somite II is found a pair of median dorsal sensillæ which are the only ones which can certainly be referred to the segmental series. This region has, therefore, been designated as somite I, a value which was first determined for it by Apathy ('88), and later, and on better grounds, by Whitman ('92). Other sense organs there are which appear suspiciously like still additional segmental organs placed anterior to those last described and sometimes separated from them by the faintest of transverse grooves. The possibility of an additional rudimentary somite in this region is suggested by these appearances, and is somewhat strengthened by indications that the brain contains four more lobes or capsules than are necessary to satisfy the requirements of the number of somites counted. In the absence of decisive evidence, these somewhat uncertain indications have been disregarded for the present, and in the tentative enumeration of the metameres here adopted, the system of Whit-

man ('92), based as it is on a careful and exhaustive analysis of the nervous system of *Glossiphonia*, has been followed. If the material were available for a similarly exhaustive study of *Microbdella*, the number of preocular somites might be augmented. The question of the constitution of this region must, I think, be regarded as still open. Although recent work has been tending toward the establishment of a typical number of segments for all leeches a great many genera still remain to be examined with requisite attention to the details. It is quite possible that leeches may vary, as all other segmented animals vary. New somites may have been added within the history of the group, just as new annul are added when the needs of greater mobility require. On the other hand, it is even more probable that the process of reduction of the number of somites below that found in primitive annelids may have continued after the establishment of the Hirudinean type, and have progressed further in some forms than in others.

The first departure from the biannulate type of somite at the posterior end occurs at somite XXIV, in which two rings can be detected only at the margins (figs. 1 and 3). The dorsal sensillæ are all present. Somite XXV is commonly a simple ring, but in the example figured (fig. 1) presented an excellent example of the spiral variation of segmentation. On the left margin a small partial annulus appears anterior to the larger one, while on the right side the latter is alone present. A very interesting circumstance concerns the position of the sensillæ on this somite. On the left side they are placed nearer to the anterior than to the posterior margin of the larger annulus, while on the normal somites, in which the relative position of the two rings is reversed, the sensillæ lie toward the posterior margin of the annulus. The next two somites are represented by simple rings, of which the first, constituting somite XXVI, is united ventrally to XXV, while XXVII is similarly coalesced with the postanal somites. Somite XXVII bounds the anus in front and may be more or less cut into by it. The anus is succeeded by two rings which are separated from each other and from somite XXVII only dorsally. As both bear metameric sensillæ they must represent somites XXVIII and XXIX. A portion of this last-mentioned somite combined with five entire somites constitute the posterior sucker. These somites are not distinguished externally, but their number was determined

by the number of ganglia in the posterior mass. Leaving out of account the possible rudimentary anterior somite the whole number counted is 34, a number which was first determined accurately by Whitman ('92), and is now generally attributed to all leeches.

Structural features of interest are not confined to the exterior, but some important characters are presented by the internal anatomy. In the first place, the intersegmental septa, which, as a result of the reduction of the cœlome, are so much modified and shifted in most leeches, are clearly represented by strong transverse sheets of vertical muscle fibres corresponding, except toward the ends of the worm, exactly with the external segmentation. Some of the septa are shown diagrammatically in figs. 4 and 5, *s*, where they are seen to begin on the ventral side exactly at the intersegmental furrows, though dorsally they tend to shift their attachments with the muscular and integumentary layers slightly forward to the smaller annulus of the preceding somite. Except where they are interrupted by the passage of organs continuing from somite to somite, the alimentary canal, principal blood vessels, longitudinal sinuses, genital ducts and nephridia, these septa are complete. The cœlome has been reduced as usual and the various organs are packed around with the usual parenchymatous tissues, glands, etc., but there are very few dorso-ventral muscle fibres except in relation to the posterior sucker. The dorso-ventral musculature of the middle region of the body is almost entirely represented by these septa, which have retained a simple structure and a primitive arrangement almost as definite and regular as in the *Oligochæta*.

Unfortunately no fresh material was available for a complete study of the nervous system by the more refined neurological methods. But by dissection, after maceration, of the preserved material, I succeeded in isolating in two examples almost the entire central nervous system, with the exception of a part of the posterior ganglionic aggregation. From these preparations and from sections the general features were determined and are represented on a small scale in fig. 5. The similarity to what is known of the nervous systems of other leeches is sufficiently evident. The anterior complex is composed of at least six and not improbably of seven neuromeres. In this region but six neuromeres were found by Whitman ('92) in *Glossiphonia* and other leeches, and by

Bristol ('98) in *Herpobdella.* The determination of the exact number in *Microbdella* is uncertain, but is based upon a count of the number of neuromeric lobes or capsules after Whitman's method. In each of the two dissections a few of these were displaced or broken, but by comparing them with each other and with sections the whole number appeared to be four greater than in either of the genera mentioned above. The distribution of the nerves of this region could not be worked out. However, I hope to be able later to state the exact number of metameres in *Microbdella.*

The seventh neuromere (still following Whitman's system of enumeration) lies very close to the subœsophageal ganglionic mass. Then follow in the ventral chain sixteen more widely separated ganglia arranged along a partially double nerve cord in the usual manner. Each of these ganglia lies principally in the major, but also partly in the minor annulus of its somite. Those from XXIV posteriorly become more and more closely crowded, the neuromeres XXVII to XXIX being especially intimately associated and practically part of the posterior complex, which is made up of very closely packed neuromeres ending as in other leeches with No. XXXIV, (fig. 5.)

Typical neuromeres of two complete somites (XII and XIII) are represented in figure 8. The six groups of nerve cells, each contained in a delicate nucleated capsule, so characteristic of the leech neuromere, are present. Four of these are arranged in pairs on the sides of the cord and the remaining two placed tandem on its ventral surface. Two nerve roots arise on each side from between the paired capsules and rather toward its ventral surface. They are bound closely together in a common sheath, so that they appear as a single nerve, on the surface of which lies a large (Leydig's ?) cell. After traversing the ventral sinus, and on entering the body walls, the two nerves completely unite, a second large cell being present at this point. From the place of union three nerve trunks arise, of which the anterior and larger (fig. 8, *v 1*) supplies the ventral portion of the larger annulus. It divides into an anterior and a posterior branch and I see no evidence whatever that these extend beyond the limits of the annulus in which they originate, but they were not traced to their end organs. A second branch (fig. 8, *v 2*) supplies the ventral part of the smaller

annulus. The third (fig. 8, *d*) arises from the dorsal surface of the enlargement formed by the union of the two roots. It passes dorsad through the parenchyma, and without doubt corresponds with the dorsal branch of the third nerve of *Glossiphonia*. In dissections it was frequently broken off short, but in some cases was sufficiently well preserved to show that it splits into a number of branches after proceeding a considerable distance as a single trunk. In sections this main nerve could be traced upward as far as the dorsal longitudinal muscles among which it was lost.

In some respects the arrangement of the nerves of *Microbdella* resembles that of *Herpobdella* (Bristol, '98) more closely than *Glossiphonia*. The attempt to point out homologies without having traced these nerves to their final distribution is no doubt open to criticism, but a comparison of the nerve trunks in the two cases is almost as convincing as though this had been done. There is little reason for doubting that the two nerve roots of *Microbdella* correspond to the two trunks of *Herpobdella*. The anterior nerve of the former corresponds with the anterior nerve of the latter, the one which supplies the ventral surface of the first ring of its own somite together with the fourth and fifth rings of the preceding somite. But Bristol has shown that this nerve is the homologue of the first and second nerves of the neuromere of *Glossophonia*, which agrees with the subdivision of the anterior nerve of *Microbdella* into two branches. The posterior nerve of *Herpobdella* is essentially like that of *Glossiphonia ;* it gives off branches to the ventral surface of the second ring of the somite in *Glossiphonia*, or to its homologue, the second and third rings of *Herpobdella*. In both genera this nerve also gives off a dorsal branch which is equivalent to the dorsal nerve of *Microbdella*. Every important element of the neuromere of *Glossiphonia* and *Herpobdella* is, therefore, represented in *Microbdella*.

The male reproductive organs (figs. 4 and 5) consist of five pairs of testes (*t 1–5*), of which the fifth is much larger than the others, and lies partly in somite XX, but chiefly in XIX. The remaining four are situated beneath as many gastric cæca in somites XV to XVIII. The majority of species of *Glossiphonidæ* have six pairs of testes, which are commonly described as being situated in somites XIII to XVIII, and although there is some discrepancy in position it may be suggested that the number preva-

lent in the family may have arisen by the subdivision of the fifth pair in *Microbdella*, or by a similar process affecting the anterior pair of an ancestral form. The primitive condition may be represented by the elongated saccular testes of *Archæobdella* (Kowalevsky, '96[a]), of which there is a single pair, by the subsequent subdivision of which the five or six pairs of the *Glossiphonidæ* may have been derived.[1] Still further subdivision would lead to the nine or ten pairs of *Hirudo*, the ten to twelve pairs of *Hæmopis* and finally to the numerous small testes of the *Herpobdellidæ*, which are so beautifully arranged to meet the structural conditions to which they must accommodate themselves. Increase in the number of testes is an accompaniment of progressive development in at least one series of leeches and is associated with increasing length of body and many correlated changes in the sperm ducts.

Another feature of the testes of *Microbdella* is the unusually large size, though this is not unique, of the sperm funnels (figs. 6 and 7). They are connected with the anterior, dorsal, mesial part of the wall of each testis and consist of cells of relatively large size. In vertical section they appear to be more or less columnar, but when cut tangentially are seen to be really flattened, somewhat plate-like cells set on edge and arranged concentrically around the mouth of the funnel. The marginal cells of the funnel pass somewhat abruptly into continuity with the excessively flattened epithelium of the testes which exhibits ciliated elevations at points corresponding to the positions of the nuclei. Toward the centre of the funnel the cells become higher, first cubical and then elevated and compressed, then again cubical as they pass through the mouth into the neck and finally change into the flattened epithelium of the vas efferens (fig. 6, *ve*). The free surfaces of all of the funnel cells are ciliated. On the more prominent parts of the funnel this ciliated area is continuous, but in the narrow neck becomes first interrupted by naked spaces and then reduced to small isolated patches of larger cilia. This latter condition becomes more emphasized within the vas efferens, where a small bunch of cilia arises on each cell opposite its nucleus. The vasa

[1] The posterior part of the testes has already become lobed and partly subdivided, so that the actual primitive condition has to this extent been lost. In this and some other features of its organization *Archæobdella* approaches the *Herpobdellidæ*.

efferentia (fig. 5, *ve*) pass vertically dorsad close to the basal part of the anterior surfaces of the gastric cæca, and in close contact with the posterior faces of the septa which limit their respective somites anteriorly. They unite above in a common vas deferens for each side. Unlike the vasa efferentia, the common sperm ducts (vasa differentia) are lined by a simple flattened non-ciliate epithelium. Their course is a perfectly straight one, without tortuosity or modification of any kind, just along the inner surface of the longitudinal muscular layer and exactly over the line of sperm funnels, as far forward as somite XII.

The vasa differentia finally terminate in the conspicuous sperm sacs (figs. 4 and 5, *ss*), which are modified enlargements of the sperm ducts, their walls being characterized by a strongly developed muscular layer and a thin lining epithelium. They have the form of a dilated tube folded into S-shape, and occupy somites XI and XII on each side of the œsophagus. The sperm sacs are not succeeded by narrow tubes (ducti ejaculatorii) of considerable length as in *Glossiphonia*, but open immediately through narrow constrictions into glandular sacs (figs. 4 and 5, *pg*). The latter rise vertically upward from the ventral ends of the sperm sacs, and after bending somewhat sharply caudad, become constricted and open into the glandular horns of the atrium (figs. 4 and 5, *at*). These horns are the terminations of the paired sperm ducts, and have a structure very similar to the section of the ducts which immediately precedes them. Each has a very narrow lumen and thick glandular walls. They may be considered as together constituting the prostates. The median atrium (*at*) which receives the openings of the sperm ducts, is a thin-walled muscular globoid sac, capable of being everted through the male pore—its external opening. The sperm sacs are packed full of mature spermatozoa in all of the specimens examined.

There is nothing especially noteworthy about the ovaries, which, within their sacs, are closely approximated and form together a massive organ lying between the nerve cord, alimentary canal and series of testes. They extend from somite XII to somite XVIII, and at the anterior end diverge from each other and form a ring through which passes the nerve cord, ventral to which they unite at the common ovarian pore (figs. 4 and 5, *ov*).

The alimentary canal is nearly like that of other small Glossi-

phonids. The protrusible pharynx (figs. 4 and 5, *ph*) extends to IX, extensible œsophagus (*œ*) to XIII, and the stomach thence to XIX, where it joins the intestine (*i*). A pair of nearly solid elongated glands are appended to the œsophagus in X (figs. 4 and 5, *g*). There are seven pairs of gastric cæca, of which the first six are small and simple and the seventh much larger and sacculated. They arise from the stomach within the major annuli of the seven somites from XIII to XIX. The first (*c 1*) bends cephalad somewhat sharply into somite XII, the next five are confined by the septa within the limits of the somites in which they arise, but they bend caudad more or less into the minor annuli and usually terminate in a bulbous enlargement (*c 4*). The seventh and last pair are continued through five somites, developing sacculations in each (*c 7*); corresponding enlargements also appear on the intestine.

Besides the position of the nephridiopores, which is described above, the only point concerning the nephridia which is worthy of comment relates to the funnels. These are very simple in structure, being composed of a single large cell. The vesicles into which they empty are formed of a small number of rather large cells. The funnels lie opposite to the outer ends of the cæca, toward their posterior dorsal surfaces, where they open into a sinus which corresponds to the complex which Oka ('94) has described in this region of *Glossiphonia* dorsal and mesiad to the lateral longitudinal sinus. They lie wholly within the minor annuli (fig. 5, *f*).

Microbdella appears to be one of those leeches in which fertilization is accomplished by the hypodermic injection of spermatozoa, a process which has been so nearly demonstrated by Whitman ('92[b]) for *Placobdella plana*. The evidence for this is found in the presence of spermatozoa in the sinuses and internal tissues of the body. The nephridial funnels and funnel vesicles are almost always gorged with spermatozoa which have been taken through the nephrostomata from the surrounding sinus. In several cases spermatozoa were found within the ovarian sacs, either aggregated in large masses or scattered among the ova. The presence of compact masses of spermatozoa in the ovaries suggests that fertilization may also be accomplished by the entrance of spermatophores directly through the ovipores. The species is protandric.

[5] There is nothing striking or distinctive about the color of this species. The body is translucent and speckled with scattered green and brown pigment cells, the general effect of which is to give the animal a pale olive green color.

The Leech Somite.—The facts contained in the foregoing description seem to me to point conclusively to a necessity for some modification of current views regarding the constitution of the typical leech somite. Most text-books of zoölogy agree in stating of leeches that external and internal metamerism do not correspond. Except in so far as this means that the somites are externally divided into rings which have no internal counterparts (a condition which is also met with in many *Oligochæta* and *Polychæta*, in which there is said to be agreement between internal and external segmentation), this is not true of *Microbdella*, for in this leech the metamerism of the exterior does correspond most exactly with the arrangement of the internal organs in typical somites.

Let us reëxamine a typical somite. Externally its boundaries are indicated by deep furrows which extend all around the body. Between these intersegmental furrows the body wall is divided into two distinct rings, which are only faintly, and in most cases partially, indicated on the ventral surface. The first ring is the larger and bears the metameric sensillæ posteriorly and the nephridiopores anteriorly. Internally well-developed dissepiments correspond with the bounding furrows exactly on the ventral side and nearly so on the dorsal. Each somite contains a ganglion of the ventral chain from which arise nerves distributed solely within the limits of that somite. There is complete agreement between the neuromeres and external segmentation. In some of the segments the ducts of the testes are in contact with the anterior septa, cæca of the alimentary canal occupy just the distance between the two septa and nephridial funnels open within the limits of one somite to pass into tubules which perforate the following septum and open on the anterior part of the succeeding somite. The external segmentation does, therefore, agree with all of the principal internal systems in which metamerism is expressed.

If, adopting the current definition of a leech somite, we similarly examine the organization of any leech which has been fully described—*Glossiphonia*, for example, as being one of the most

simple and best known—the chief discrepancy is found to exist between the arrangement of the nervous system and the groups of rings which indicate the somites externally. The two anterior rings of each somite are innervated by its own neuromere, and its third by the immediately succeeding neuromere, or, as Whitman ('92) has stated it, the peripheral nerves of typical somites "innervate three successive rings, the first and second of their own segment and the third of the preceding segment. The distribution is thus triannulate and dimeric." The body walls have, so to speak, slipped one ring backward on the nervous system or the nervous system one ring forward on the body walls.

Can it be possible that there is such a fundamental difference between two genera of leeches of the same family as would exist if both of the above interpretations are correct, and if not, which of the two interpretations must be accepted? An attempt to reply to these questions necessitates a close comparison between typical somites of the two genera. The most striking external difference is that the somite of *Glossiphonia* is triannulate, while that of *Microbdella* is only biannulate. As each has one ring bearing metameric sensillæ, the difference appears to be that *Microbdella* has one less ring lacking segmental sense organs than has *Glossiphonia.* There are no known external marks which constantly belong to the latter rings throughout the different genera, but the comparison of the nerve supply already given shows that the second annulus of *Microbdella* finds its counterpart in the ring of *Glossiphonia* which succeeds the sensilliferous one, for in the former genus there is no ring which receives its nerve supply from the succeeding neuromere, while the nerves which supply the second annulus in the two genera have been shown to be homologous.

The sensillæ-bearing annuli of the two genera under comparison resemble each other, in addition to the presence of the sense organs, in containing the nerve ganglion and nephridiopores,[2] and according to the accepted interpretation in being the most anterior of their somites. Without further examination it might therefore be concluded that these rings are homologous, that the biannulate

[2] The description of *Clepsine hollensis* Whitman is mainly being followed. In some other allied species the nephridiopores are on the boundary between this and the preceding annulus.

somite is equivalent to the first and second rings of the triannulate type, that the posterior ring of the latter is unrepresented in the former, and that the want of a nerve supply from the succeeding ganglion is correlated with its absence. But the sensillæ-bearing annulus of *Microbdella* is not in all respects like that of *Glossiphonia*. In the first place it is much larger than its fellow-annulus in the somite, while in *Glossiphonia* the annuli are of equal size or the sensillæ-bearing one somewhat smaller than its mates. It has been repeatedly shown by Whitman and Apathy and by many others in a great variety of leeches that all the annuli of a given species of leech are not equivalent, that a single annulus toward the end of the body may represent two or more annuli of a somite in the middle region. Such annuli almost invariably indicate their greater value by a larger size as compared with those adjacent. This fact alone should make it evident that the sensillæ-bearing annulus of *Microbdella* comprehends more than that of *Glossiphonia*. This additional part cannot be the middle annulus of *Glossiphonia*, for this has already been shown to have its exact counterpart, both in position and nerve supply, in the minor annulus of *Microbdella*. Just as certainly does the posterior position of the sensillæ indicate a greater value for the part of the ring in front than behind them and lead us to look for the missing member in a more anterior position, and consequently within the preceding somite of *Glossiphonia*. Comparison of the nerve supply locates it in the third annulus, for it will be remembered that the anterior part of the larger annulus of *Microbdella* is supplied by a nerve homologous with the one which in *Glossiphonia* reaches into the preceding annulus. The major annulus of *Microbdella* is equivalent, therefore, to the sensillæ-bearing annulus plus the one which precedes it in *Glossiphonia;* the first is represented approximately by that portion of the major annulus which bears the sensillæ and lies caudad of the nephridiopores and the second by the cephalic portion. Occasionally a very faint groove partially marks the boundary line.

If the limits of the somites of leeches have been hitherto correctly defined then *Microbdella* is a leech in which every somite throughout almost its entire length has obviously given up its posterior third to the following somite and absorbed the corresponding third of the preceding somite, a suggestion which is so improbable

that it might almost be repudiated without examination. But the fact that the entire bodily organization, and especially the distribution of the nerves, point to the external metamerism of *Microbdella* as fundamental is sufficient to dispel any lingering suspicion with which we might be led to regard an animal which is very small and parasitic, and therefore a likely subject for degeneration. On the other hand, the lack of alignment between the neuromeres and external segments as hitherto determined argues forcibly against the current view. The interpretation of the structure of *Microbdella* shows, therefore, that the sensillæ-bearing annulus is the middle and not the first of the triannulate and quinqueannulate somites, and that we must look for agreement between the distribution of the nerves and the external segmentation in all leeches.[3] That the neuromeres cannot be an absolute criterion of the limits of all of the somites has, of course, been shown by Whitman for *Glossiphonia* ('92), in which the peripheral nerves of the anterior neuromeres shift and unite in such a manner as to obscure their segmental value. But this fact does not lessen their utility for determining the typical somites.

Since the above conclusions were reached about eighteen months ago, I have examined many genera and species in order to apply this new interpretation to their external segmentation, and in search of corroborative evidence. The latter has been ample; but the details are too voluminous for statement here and now. That the new standard of enumeration accords better with the facts and explains away some of the difficulties now found in all families of leeches is evident from the following general statements. The increasing simplicity of the somites from the middle toward the ends of the body becomes more gradual and regular; adjacent somites differ from one another by seldom more than one ring, whereas under the current system there are sudden jumps from five to three to one, etc. Moreover the individual somites almost invariably repeat the condition of the entire extremity in which they are located; their distal ends present (especially when the whole number of annuli is less than the typical number for the species) a less devel-

[3] After this paper had been written and presented for publication, Castle (Abstract of papers read at the New Haven meeting of the Morphological Society, *Science*, February 2, 1900, p. 175) announced his arrival at precisely the same conclusion. It is a real pleasure to be able to furnish such complete confirmation of results as carefully worked out as were Castle's.

oped condition than their proximal. The necessity for splitting rings—dividing the halves between two contiguous somites—practically disappears, for union of the rings of neighboring somites consisting of more than a single annulus each, is exceedingly rare, if indeed it ever occurs; division into somites is far more fundamental than division into rings, which have no primary metameric significance, and is never, or very rarely, obscured by the latter. The shifting of the sensillæ back and forth on the ring which bears them, as the balance of growth is thrown, with the splitting off of new rings, first on one side, then on the other, takes place exactly as it should if the present view is true, while it is inexplicable upon that hitherto accepted, in fact, contradictory of it. The same is true of many of the cases of spiral annulation and partial annulation which have been studied; and none have been found to favor the current view, while opposing the one here upheld. Very curiously the left side of somite XXV of fig. 1, representing the only important variation met with among the twelve examples of this species, illustrates the last two statements. If the sensillæ-bearing annulus be really the first of all leeches, why does the partial ring appear anterior to it, and why do the sensillæ of that side move forward? If the sensillæ belong primarily to the middle of the somite, the insertion of an anterior ring is perfectly natural and the change in position of the sensillæ the result of a readjustment of the ring to the new balance of growth. The differences in the location of the nephridiopores in different genera and families is a difficulty which others have recognized and tried to explain as a result of shifting or the disappearance of annuli. Upon the view here held the nephridiopores always fall within the same region of the somite and have shifted back and forth only within limits which might have been expected. The change in the position of the septa during ontogeny appears to be confirmatory, but this evidence is still rather obscure and unsatisfactory. A better explanation of the position of the intermuscular nerve rings described by Bristol in *Herpobdella* seems to be afforded.

But one[4] serious objection to the application of this neuromeric

[4] It has not been thought necessary to regard Blanchard's ('98) determination of the large double annulus of *Torix* as the posterior one, as an objection. This conclusion was arrived at without any knowledge of the

standard has been met with. In certain genera of leeches both sex-pores would fall within the limits of somite XII, whereas under the current system the male pore is in XI and the female in XII. This condition occurs very rarely outside of the family *Herpobdellidæ*, in which the sex pores are peculiarly liable to variation both between species and among individuals of the same species. Six out of seven North American species have them separated by two rings. In European species they are from two to five rings apart. In the genus *Orobdella* of Japan, Oka ('95) has described a variable number of rings as intervening, but the distance amounts to more than a full somite. Still more remarkable are the individual variations, among which it is not uncommon to find the two sperm-ducts, instead of opening together, with distinct apertures separated by one or even two full rings. These facts and others indicate that the pores are shifting their positions and it is along this line that a solution of the difficulty is being sought.

It is a matter of some morphological importance to find a standard by which the leech somite may be correctly delimited, and the present writer's chief interest is connected with the possibility which now exists for the first time, of making a detailed comparison between the Hirudinean and Oligochæte somites, a comparison which, it is believed, will do much to bring the two groups closer together and to weaken the position which is still adhered to by some eminent authorities that the *Hirudinea* were Platyhelminthine in origin. How the general theory of metamerism will be affected has not yet been considered.

The adoption of this standard will also necessitate the modification of the generic formulæ which were proposed in my paper on "Leeches of the National Museum" ('98). The theoretical formula may remain the same for leeches with three annuli and over, but the discovery of a more primitive biannulate form destroys some of its significance, and the annuli which undergo most elaboration must now be designated as *a 1* and *a 3* instead of *a 2* and

position of the nephridiopores or sensillæ or other intrinsic data for the determination of the limits of the somite. It is an assumption from the accepted theory and practice. When *Torix* is studied by means of sections it seems very probable that the nephridiopores will be found in the anterior half and the sensillæ on the posterior half of the double annulus. Should this surmise prove to be incorrect, *Torix* will probably present a serious obstacle to the acceptance of the conclusions suggested by the structure of *Microbdella*.

a 3, while *a 2*, which becomes the symbol for the middle sensillæ-bearing annulus, remains relatively stable.

The number of annuli into which typical somites are divided, together with the number and degree of departures from this type in a given form of leech have been much used in classification. Whitman and Apathy especially have considered these characters as of great phylogenetic significance. But the fundamental conceptions of these two zoölogists regarding the meaning of the facts belonging to the first-mentioned class are diametrically opposed. Up to now leeches have been known whose complete somites contained from three (two dorsally in *Torix*) to fourteen (twelve according to Apathy's count) annuli. Apathy ('88) believes that the latter is the primitive number and that all other types have been derived from this by a process of absorption and suppression of those rings which have lost their functional importance in the evolution of genera from a purely parasitic form to forms which have become adapted to a variety of environments. Whitman (90[a] and elsewhere) considers the triannulate type as the primitive one from which the multiannulate somites of the *Gnathobdellida* are derived by a process of progressive fission and multiplication of rings. The latter view seems to be most in accord with the facts of embryology and comparative anatomy and has been supported by several zoölogists, including the present writer.

It is well known that typical complete somites are absent from the end regions of nearly all leeches, where they are represented by somites which contain a smaller number of rings. Whitman, Apathy, and I believe all other modern writers on the *Hirudinea* are agreed that such somites, when of less than three rings, are the result of a process of reduction, that uniannulate or biannulate somites occurring in a typically triannulate leech have been derived from the latter type of somite by a process which is essentially one of phylogenetic concrescence—a shrinking in size of the affected rings, together with a smoothing out of the furrows which genetically separate them. The favorable argument seems to be derived largely from analogy to other groups of segmented animals and it must be admitted has seemed to explain the facts known up to the present time. Whitman, who is the author of this hypothesis, has formulated it as follows:

"All somites with less than three rings are abbreviated, and

all with more than three have been increased by the division of one or two of the three primary rings. I have collected considerable evidence, which cannot be given here, to show that in the evolution of *Hirudo*, it was the second and third rings that underwent division, while the first remained undivided" ('92, p. 392). Probably the authors of the opinions that the triannulate or multiannulate somites represent the primitive types would admit the probability of the occurrence of a uniannulate ancestor somewhere in the remote history of the *Hirudinea*, but evidently no such form was looked for within the limits of the group. Blanchard ('98), to whose activity in systematic studies we owe the discovery of so many important generic types of leeches, describes the typical somite of *Torix* as biannulate with one ring subdivided into two on the ventral surface. This type of somite he regards as more primitive than that of *Glossiphonia*, and prophesies the discovery of a uniannulate leech, a prophecy which *Microbdella* so nearly fulfils. The discovery of a truly biannulate leech sheds new light on the subject, and it seems very doubtful if Prof. Whitman himself would explain this condition as a process of abbreviation affecting all of the somites of the body, and most of them in a perfectly similar manner and to an equal degree. The variation shown in the somite XXV of fig. 1 affords, however, one little bit of evidence for such a contention, for it is indeed very curious that the only distinct attempt toward the separation of annulus *a 1* should occur in a somite which is in other respects of simpler structure than the type. I have no explanation or excuse to offer for this bit of wilfulness upon the part of my material.[5] The crucial question is really which is the most primitive in structure, *Glossiphonia* or *Microbdella*. If the former shows evidence in its general organization of standing nearer to the ancestral Hirudinean stock, then the biannulate somite has probably been derived by abbreviation of the triannulate. If *Microbdella* proves to be the more generalized, the converse is probably true. In the general description reason has been given for believing that the latter is true. The evidence is found chiefly in the exact agreement between the metameres as expressed internally and externally

[5] There is evidence that this and some similar variations may be the result of a conflict between immediate mechanical factors and hereditary influences.

by the different systems of organs, and in the structure and arrangement of the dissepiments, testes and nephridia. The few specialized characters are unimportant and easily explained. It is therefore concluded that *Microbdella* approaches nearer to and throws light upon the characters of a primitive ancestral leech which phylogenetically preceded the *Glossiphonidæ*, etc. The triannulate somite of the latter has, therefore, been derived from a biannulate somite. The derivation of the multiannulate from the triannulate type is but the continuation of the general process of elaboration begun earlier, and which affords a means of maintaining the flexibility of the body as it increases in length.

The structure of *Acanthobdella* (Kowalevsky, '96[b]), which is a true annectant type between *Hirudinea* and *Oligochæta*, seems to present a difficulty, as this leech appears to have quinqueannulate somites, but the discussion of this remarkable form can profitably be postponed until the publication of Kowalevsky's final paper, which has not, I believe, yet appeared.

Microbdella also furnishes some data which seem to make it sufficiently clear that in the development of the triannulate from the uniannulate somite (if such a type actually existed), the latter first became enlarged posterior to the segmental sense organs, a posterior ring was then split off which became the third (*a 3*). The anterior part of the then biannulate somite grew and a furrow was formed approximately in the plane of the nephridiopores, thus producing the first ring (*a 1*) and leaving the sensillæ on the second (*a 2*). Some direct evidence of an embryological nature, and a considerable amount of collateral evidence derived from comparative anatomy and relating chiefly to the relative positions of the internal organs in a number of genera has been collected in support of this view, but cannot be given here.

The conclusion arrived at that the triannulate has been reached through the biannulate somite leads to one further consideration. Are the uni- and biannulate somites which are so generally found toward the ends of the body in nearly, if not quite, all leeches the product of abbreviation as now universally admitted ? The answer is in large part a corollary from the above conclusion, but the very fact of the occurrence of one or several biannulate somites[6]

[6] Such somites are not usually apparent by the current manner of counting, as the larger rings have very often been interpreted as indicating fusions of contiguous parts of neighboring somites.

having all of the essential characteristics of the typical somite of *Microbdella* in both the anterior and posterior ends of nearly all leeches is in itself very significant. The argument then is the same as that adopted by Whitman ('92) to show that the triannulate somites of the *Hirudinidæ* are "type somites" and not "abbreviated somites." It is therefore believed that the smaller number of rings embraced by the somites toward the ends of a leech's body is not due to their having been reduced from the condition of complete somites, but that most of them represent phylogenetic stages of development arrested or still in progress toward the complete type. We may therefore read one part, and this no doubt much garbled, of the story of a leech's ancestry in the records of its somites from the extremities toward the middle of its body. There are, of course, other versions of this story which are recorded elsewhere. It is not meant to be implied that the retrograde process of abbreviation has never occurred in the differentiation of the genera of leeches, as some almost certain cases of this are known, but it is believed that they are infrequent and that the process has not played anything like the important part which has been attributed to it. Nor must it be supposed that a leech which presents a large number of incomplete somites is regarded as necessarily primitive, for it is recognized that specialization of somites may take place, and has taken place, in other ways than by an increase in the number of rings, for example, by a great development of segmental sense organs, as in the *Hirudinidæ*.

The difference (in respect to the number of component rings) between somites of the middle and terminal regions of a leech's body is believed to have arisen phylogenetically by a process which is more accurately described as one of centrifugal expansion and elaboration rather than "centripetal abbreviation." The somites of the middle region probably first increased in size and multiplied their annuli and in this region the process has advanced the farthest. From this centre the change has extended toward the ends, but with gradually diminishing effect. The terminal somites, already specialized in other directions, might be positively lowered in efficiency by any increase in length.

List of Papers Cited.

Apathy, Stefan. '88. Analyse der äusseren Körperform der Hirudineen. Mittheil. zool. Sta. Neapel, viii (1888), 153–232.

Blanchard, R. '98. Noveau type d'Hirudinée (*Torix mirus*). Bull. Scient. France et Belgique. xxviii (1898), 339–344.

Bristol, Charles L. '98. The Metamerism of Nephelis. Jour. Morph., xv (1898), 17–72.

Kowalevsky, A. '96[a]. Étude sur l'anatomie de l'Archæobdella Esmontii de O. Grimm. Bull. Acad. Imp. Sci. St. Petersbourg, v (1896), 331–335. Comm. prélim.

Kowalevsky, A. '96[b]. Étude sur l'anatomie de l'Acanthobdella peledina. Comm. prélim. Bull. Acad. Imp. Sci. St. Petersbourg, v (1896), 263–274.

Moore, J. Percy. '98. The Leeches of the U. S. National Museum. Pro. U. S. Nat. Mus., xxi (1898), 543–563.

Oka, Asajiro. '94. Beiträge zur Anatomie der Clepsine. Zeitschr. f. wiss. Zool., lviii (1894), 79–151.

Oka, Asajiro. '95. On Some New Japanese Land Leeches. Jour. Coll. of Sci. Imp. Univ. of Japan, viii (1895), 275–306.

Whitman, C. O. '86. The Leeches of Japan. Part I. Quar. Jour. Micr. Sci., xxvi (1886), 317–416.

Whitman, C. O. '90[a]. Description of Clepsine plana. Jour. Morph., iv (1890–91), 407–416.

Whitman, C. O. '90[b]. Spermatophores as a means of Hypodermic Impregnation. Jour. Morph., iv (1890–91), 361–405.

Whitman, C. O. '92. The Metamerism of Clepsine. Festschr. zu. 70ten Geburtstage R. Leuckarts (1892), 385–395.

EXPLANATION OF PLATE VI.

Microbdella biannulata.

Figs. 1, 2 and 3. Dorsal, ventral and lateral views, respectively, of a full grown, partly extended specimen, showing the chief external characters. × (about) 15. I to XXVII, the twenty-seven preanal somites; *m*, mouth; *a*, anus; *e*, the ocular pigment spot; ♂, male pore; ♀, female pore; small circles indicate the segmental sensillæ and dots (in fig. 2) the nephridiopores.

Fig. 4. A semi-diagrammatic representation of some of the more important features of the alimentary canal, organs of reproduction and dissepiments as seen from the dorsum. The entire digestive tract is outlined and the reproductive organs are seen as though it were transparent. The sperm sacs are displaced laterally in order to expose the atrium. The parenchyma and other filling tissues are

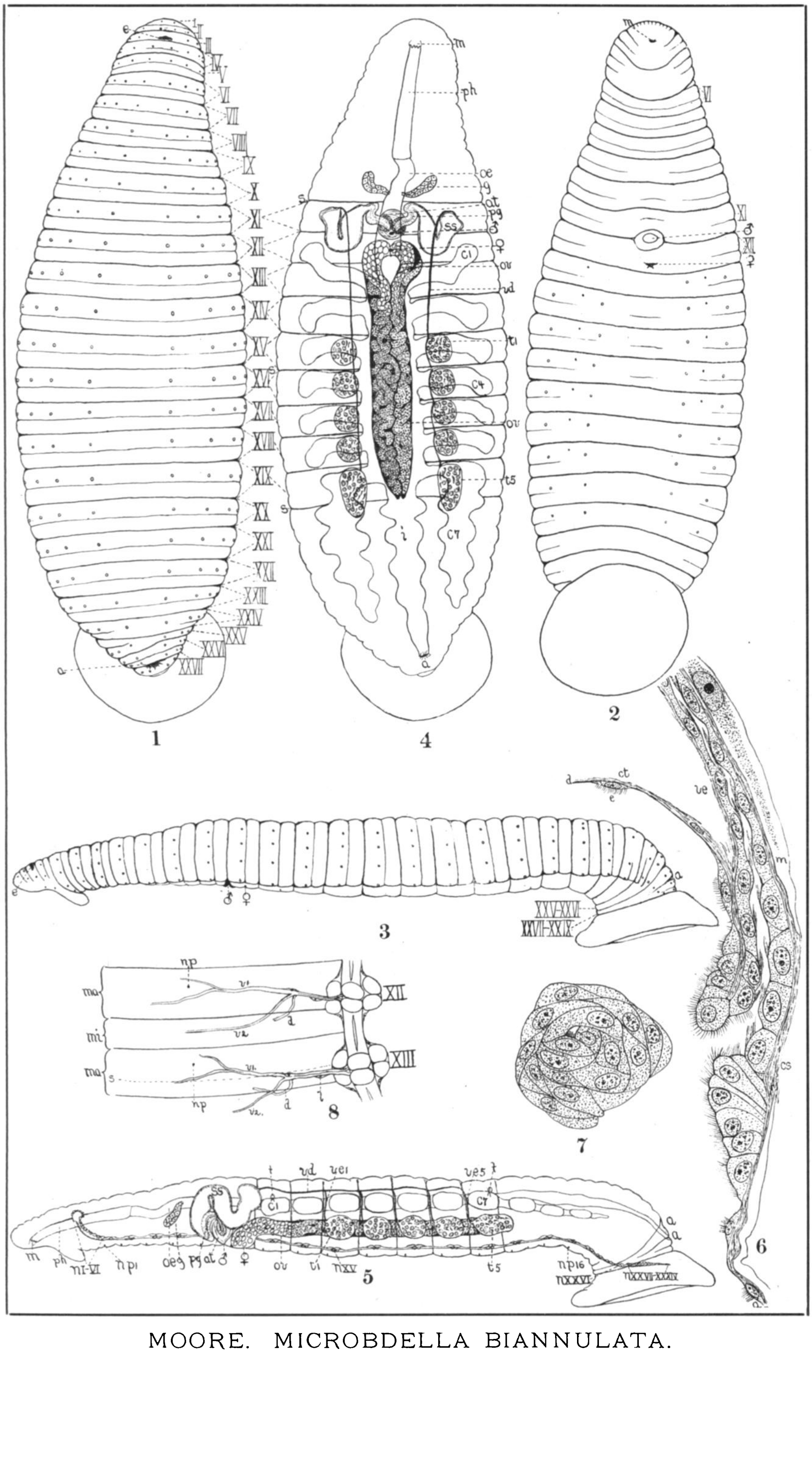
left out of account. × 15. *m*, mouth; *ph*, pharynx; *œ*, œsophagus; *g*, œsophageal glands; *c 1–7*, the seven pairs of gastric cæca; *i*, intestine; *a*, anus; ♂, male pore; *a*, median atrium; *pg*, prostate sac and gland; *ss*, sperm reservoir; *vd*, vas deferens; *t 1–5*, the five pairs of testes; ♀, female genital pore; *ov*, ovaries and their ducts (the arrangement of the loops of the egg-strings is purely diagrammatic); *s*, the muscular dissepiments corresponding to the anterior limits of somites XI to XX.

Fig. 5. A lateral view similar to fig. 4, and showing in addition the entire length of the central nervous system, the positions of the nephridiopores and of two of the nephridial funnels. The sperm sac has been displaced slightly caudad. The lettering is the same as in fig. 4, with the following additions: *n I–VI, XV, XXVI* and *XXVII–XXXIV*, neuromeres as numbered; *np 1–16*, nephridiopores 1 to 16; *f*, funnels of nephridia; *ve 1–5*, the five vasa efferentia.

Fig. 6. A vertical longitudinal section through a sperm funnel of the last pair, showing the continuity of its cells with the testicular epithelium on the one hand, and with its vas efferens on the other, and the contact of the latter with the muscular septum. The testes, of course, faces to the right instead of the left as in fig. 5. × 300. *d*, dorsal wall of testes, with *e*, its lining epithelium, and *ct*, its connective tissue tunic; *a*, anterior wall of testes; *m*, muscle fibres, and *cs*, connective tissue of septum; *ve*, ciliated epithelium of vas efferens.

Fig. 7. A tangential section across a sperm funnel, showing the concentric arrangement of the cells around the contracted mouth. × 300.

Fig. 8. Two typical neuromeres, XII and XIII, showing the principal nerve trunks and their relation to the annuli, etc. × 35. *ma*, major, and *mi*, minor annulus; *s*, position of the row of metameric sensillæ; *np*, position of nephridiopore; *v 1*, anterior, *v 2*, posterior, and *d*, dorsal nerve trunks; *l*, Leydig's (?) cells.



MOORE. MICROBDELLA BIANNULATA.